Animal Breeding Programs: Systematic Approach to their Design

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Abstract

This publication presents a systematic nine-step approach to designing comprehensive animal-breeding programs. These nine steps are (1) describing the production system(s), (2) formulating the objective of the system, (3) choosing breeding system and breeds, (4) estimating selection parameters and economic weights, (5) designing an animal evaluation system, (6) developing selection criteria, (7) designing matings for selected animals, (8) designing a system for expansion, and (9) comparing alternative combined programs. Formulating the objective (step 2) may be in both simplified and comprehensive forms. This nine-step approach is also a basis for developing computer models for analyzing alternative breeding and selection systems. Principles and procedures, including iterative and branched approaches, and the difficulties in designing and implementing coordinated breeding strategies in segmented industries are also reviewed.

Keywords: systems approach, animal breeding, genetic improvement, crossbreeding, selection, design, planning

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Animal Breeding Programs: A Systematic Approach to their Design[1]

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Introduction

Designing comprehensive animal breeding programs for a specific objective is complex. Often, breeders are overwhelmed by the details that must be evaluated before making the numerous decisions. Too many breeding programs do not have adequate specification of details of the design. They also have overly simplified objectives. This is true even though numerous scientific studies have been reported on the two primary tools available to the breeder—responses to selection and consequences of crossbreeding.

These inadequacies can be overcome by an organized process for integrating the available knowledge into comprehensive plans that can be systematically implemented. In this publication, we present a procedure for methodically dealing with the myriad of details involved in developing comprehensive breeding programs. Choices, decisions, and other relevant information to develop a breeding program are arranged into eight groups, or steps, in a natural sequence. The later groups in the sequence are dependent upon the information developed in earlier groups. A ninth step allows a more comprehensive comparison of alternative designs and allows departures from the strict sequential structure. Our goals in developing these steps were to provide an organized methodology for breeding-system design without restricting the creativity in the decision making.

In this study we took a general approach that is applicable to all classes of livestock and to relevant breeding objectives for each class. The planning decisions made in each step will differ, however, because of special characteristics and purposes of each case. We did not reach specific decisions for particular classes of livestock but describe the basis for doing so.

Recommended Steps for Designing a Comprehensive System

Ideally, the steps outlined here should be carried out sequentially from 1 through 8. The requirements of the later steps need to be anticipated fully in the earlier steps. If the earlier steps are not dealt with fully in the beginning, they will need to be revised until all steps are mutually compatible. These eight steps and how they relate to each other are discussed in detail in the following sections:

- Step 1. Describe the production system(s)
- Step 2. Formulate the objective—both simplified and comprehensive—of the system
- Step 3. Choose a breeding system and breeds
- Step 4. Estimate selection parameters and economic weights
- Step 5. Design an animal evaluation system
- Step 6. Develop selection criteria
- Step 7. Design matings for selected animals
- Step 8. Design a system for expansion

In addition, the animal-breeding theory, technology, and procedures available for making decisions are reviewed. Approaches are suggested where gaps exist in available procedures. Because of the broad nature of these steps, most animal breeding research of the past several decades is relevant. Thus, we did not make a comprehensive review but cite key general references pertinent to the suggested approach. Often, complete decision making will be neither possible nor desirable in the sequence of the eight steps. A final step, then, Step 9, **Compare Alternative Combined Programs,** will be added to allow broad decisions not possible in the earlier steps.

Step 1. Describe the Production System(s)

In this description, use numerical specification and include environments and marketing situations that are to be targets of the breeding program. Specify livestock species, products and purposes, and geographical and climatic areas of interest, and emphasize the benefit and cost considerations. This description should include the normal life cycle of parents and production animals specifying ages for breeding; timing of offspring production; expected fertility and fecundity; ages or weights for weaning, intensive feeding, marketing, and slaughter; and all other relevant and important points in the life cycle. The nature of feed, labor, land, buildings and equipment requirements, and the corresponding costs in the various stages, is necessary to fully describe the system.

For some classes of livestock, this step may be complicated by the several alternative, but simultaneously relevant, systems for production that result from tailoring a production system to the resources in a specific location or production unit. For example, the length of grazing periods and the length of intensive feeding periods change because of the differential availability and cost of feed

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relative to grass in different geographical or climatic areas. When such differences in management systems exist, all potential systems should be assessed and described, and the relative frequency of each included in the overall description. In meat-producing livestock, both the parent animals and their offspring are involved in the production system and often have different owners at different times in the production cycle. All these involvements should be included in the total production system.

In addition, the flow of genetic material between the selection segment and the production segment of the industry should be considered. Even though the plan may be changed or modified in step 8 (expansion), the system in use (or lack of system) should be assessed. A generalized pyramid relevant for all production classes of livestock (fig. 1) shows the six functions that should be involved in the complete assessment of the production system with a sequential genetic flow from top to bottom. The primary purpose of selection at the apex of the pyramid or of crossbreeding in the center must be to improve the efficiency of the lower functions of reproduction, production, and processing.

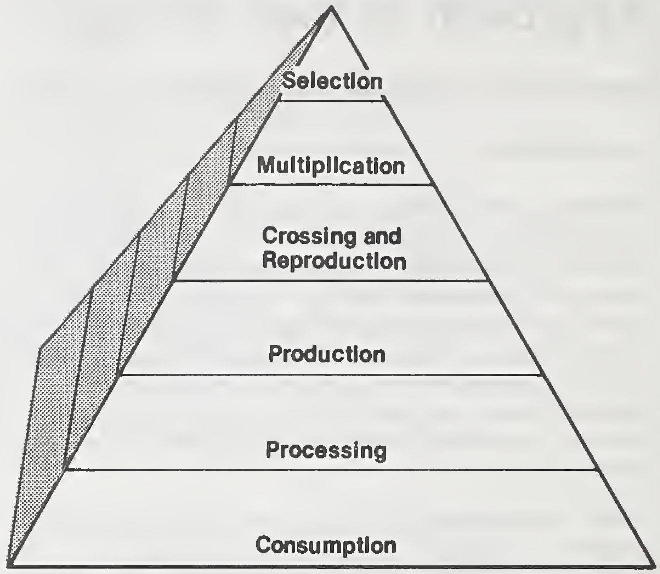

Figure 1.—The major sequential aspects of comprehensive livestock production systems where genetic improvements should flow from the top of the pyramid to the base.

Cartwright (1979) reviewed the principles relevant to describing animal-breeding systems. Sanders and Cartwright (1979a, 1979b) similarly described the principles specific to beef cattle.

Step 2. Formulate the Objective of the System

The objective should be determined as a mathematical function or set of functions that describes the contributions of various aspects of the system (especially the genetic aspects) to its productive efficiency. This determination may also serve to evaluate the impacts of alternative management and nutrition schemes on the system. The focus should be upon the specific segment of the industry affected by the specific breeding program being planned. In this step, the description in words from step 1 is converted into a more exact mathematical form to quantify the net impact of genetic and other changes in the efficiency of the system(s).

The objective of the system(s) is best defined in two forms: a simplified objective for the production units and a comprehensive objective of the complete integrated system. Both objectives should describe the total efficiency of parental lifetime reproductive performance along with the efficiency of production from (crossbred?) offspring. They also should include the relative economic importance of all the component traits as expressed in the contribution of production animals (parent and offspring) to the efficiency or profitability of the enterprise.

Form A. Formulate Simplified Objective for Production Units—Develop a simplified objective focused at the performance characteristics for production units of parent females and their offspring (with appropriate consideration given to the costs of mating). This simplified form is necessary to implement the optimization procedures for step 6 (criteria) and may be an adequate basis for other decisions. The form should be expressed as a single linear or quadratic function, involving the component traits with coefficients that represent the relative economic importance of the production unit characteristics involved. If most of the animals in the system are the production animals and their parents, this simplified objective should approximate accurately the more complex objective. If more than one production system was specified in step 1, the objective should focus on either the major or the average system. The average system would include each type of system, weighted by its frequency of occurrence.

In developing a mathematical description of the objective, it is difficult to achieve an appropriate balance between the complexity of the description necessary for complete inclusion of the relative importance of all components of a total breeding and production program and the simplicity necessary to facilitate certain steps in this planning scheme. For step 2 (form B), we encourage a comprehensive definition of the bioeconomic objective with appropriate mathematical complexity. Smith (1936) and Hazel (1943), however, developed the procedures for constructing selection indexes that are linear functions of component traits when the economic objective is a linear function of the genotypic values for the traits. This theory was elaborated upon by Cochran (1951) and Henderson (1963). Wilton et al. (1968) extended the procedure to include quadratic selection indexes for improving quadratic functions of the component traits when their distributions are normal.

Optimum procedures are available for developing linear or quadratic selection criteria for step 6 when the objective of selection is of a linear or quadratic mathematical form. When the comprehensive objective is not expressed in this simple form, as usually is the case, it is desirable to develop a **simplified** approximate function of this form to facilitate the construction of selection indexes. Over simplification, however, may lead to an inadequate representation of the importance of nonlinear interactions between component traits or to inadequate inclusion of the costs of selection or multiplication schemes. The risk seems small when compared with the value of the optimization procedures for steps 6 (criteria) and 7 (mating).

Along with a simplified mathematical form, a simplified representation of the system can be achieved by evaluating only the performance of basic production units. For meat animals, an appropriate basic production unit would be a parent female and all her offspring, including the fraction of the male(s) necessary for her reproduction. For dairy animals or egg production poultry, the production unit could be only the specific animal producing the milk or eggs, but with a description of the cost of producing that individual (which would result from the parent's reproductive efficiencies). A more complete production unit would include a maternal grandparent female, her female progeny (female parents), and her grandoffspring. Thus, a **simplified** quadratic or linear function for the performance of the basic production units is needed here for use in steps 5, 6, and 7 to determine the effectiveness of the selection program in improving the efficiency of the fundamental production units. The efficiencies of such production units will include a major portion of the efficiency of the total industry segment served by the specific breeding program, especially in classes of livestock in which the reproductive rate allows the majority of the animals to be production animals.

The contribution of a specific production unit to making the enterprise profitable can be approximated easily by a quadratic function because profit is a linear function of mathematical products of the primary traits. As an example, the profit for a meat animal dam and her offspring (fixed breeding seasons and constant interval postweaning growth period) can be expanded without serious oversimplification as follows:

$$\mathbf{L\,N\,[(W+G\,d)\,V-d\,(G\,C\,f+t)]\,-\,(p-s)\,-\,L\,(x+N\,y)} \quad (1)$$

where **L** is the length of reproductive life in number of breeding seasons,
N is the average number of offspring weaned or produced per breeding season,
W is the average weaning weight of offspring,
G is the average daily gain for the postweaning period,
d is the length of the postweaning growing period in days (constant),
V is the value per unit weight resulting from carcass composition,
C is the feed-to-gain conversion ratio for postweaning growth,
f is the cost per unit feed,
t is the nonfeed costs for postweaning growth per day,
p is the cost of the ready-to-mate dam,
s is the salvage value for the dam,
x is the dams costs per breeding cycle (including mating costs),
y is the additional (above x) preweaning costs per weanling animal.

(In this function, capital letters indicate traits of primary interest because of their impact upon profit, and lowercased letters indicate economic constants.) The economic constants **p, s, x,** and **y** might be developed further as functions of traits of interest. Each trait may be expanded as a mean plus a deviation ($\mu + \delta$) with appropriate subscripts, for example, $\mathbf{L} = \mu_L + \delta_L$.

Expanding and rearranging this function will yield individual terms involving one, two, three, or more δ values multiplied together. Deleting terms with three or more δ values multiplied together leaves a quadratic function of the δ deviations (changes in component traits) to approximate the above more complex function. By retaining only the terms with single δ values, one would have a linear approximation for the changes in component traits. The coefficients of these deviations will be linear functions of mathematical products of one or more means for other traits and the economic constants. For example, the coefficient of δ_N for the described development would be

$$\mu_L\,[(\mu_W + \mu_G\,\mathbf{d})\,\mu_V - \mathbf{d}(\mu_G\,\mu_C\,\mathbf{f} + \mathbf{t}) - \mathbf{y}]\,. \quad (2)$$

These functions reflect the relative economic importance of changes in the traits and can be the economic weights of Hazel (1943) for which numerical values will be developed in step 4 (estimation). Terms with squared δ values give the primary curvilinearity of the relationship and terms with products of two different δ values describe interactions. Higher order curvilinearity and interaction, however, are ignored with the deletion of higher order terms. In this example, there are no squared terms but many product terms. Because the exact values for the means are not known until after step 3 (breeding system), the specification of precise numerical values for these coefficients must be delayed until step 4.

Form B. Formulate Comprehensive Objective of Integrated System—Even though the simplified objective might suffice for some later steps, another form for the objective seems desirable for other steps. The simplified objective does not include two aspects of the total program that might be of considerable importance in making program decisions: (1) costs of the evaluation and selection program (steps 5 and 6), and (2) effectiveness of the purebreeding or crossbreeding program (step 3) and the expansion program (step 8). These aspects are more important when considering classes of livestock with low reproductive rates so that only one-half to two-thirds of the animals in the total system are described by the simplified objective. Although involving details of the **p** term of the simplified form, these aspects require considerable mathe-

matical complexity for complete expression. For example, multiple mathematical equations may be more feasible than arranging the mathematical descriptions into a single equation.

Dickerson (1970) emphasized the desirability of expressing the objective in the form of cost-per-unit product, which is a ratio of two functions of characteristics of the system. Alternatively, Cartwright (1970) prefers the ratio, offtake per unit input, to express the objective. There are compelling reasons for expressing the objective as one of these ratios; however, a ratio is not amenable to available procedures for step 6 (criteria) unless it can be approximated by a linear or quadratic function. Such a ratio, however, could and probably should be utilized in making step 9 comparisons and in predicting the expected impact of a specific breeding strategy. Considerations of a total breeding and production system over a long period involving cash flow and discounting are not easily amenable to the procedures currently available for step 6. All these mathematical complexities may, on the other hand, be useful in a comprehensive description of the objective to be used as a basis for the comprehensive calculations for step 9.

Because breeding is a long process, the objectives should remain pertinent for several generations. Changes should be predicted in the relative economic importance of alternative characteristics as well as in management systems. Prediction is not always possible, however, and the best indicator of future economic situations may be current economic situations. In such a case, the breeding-system designer should attempt to use economic evaluations that reflect stable current conditions and avoid seasonal and cyclical irregularities in marketing and purchasing.

During the past 15 years, many researchers reported on the methodology and implications of defining breeding objectives. General principles were reviewed by Dickerson (1970, 1976), Harris (1970), Hill (1971), Miller and Pearson (1979), and Danell (1980). The impact of long-term aspects and discounting was discussed by Hill (1971), Smith (1978), James (1978), and Bird and Mitchell (1980). Several researchers considered the objectives, organization, and other aspects of pig-breeding programs: Legault and Ollivier (1974), Fowler et al. (1976), Bichard (1977), Lindhe and Holmquist-Arbrandt (1977), and Siler et al. (1977). Similarly, Cunningham (1974) and McClintock and Cunningham (1974) studied the aims of dairy cattle breeding. The specific value of body size in the objective was reviewed by Morris and Wilton (1977) and Dickerson (1978). An informative discussion of the differential emphasis for selection in sire and dam lines is found in the series of papers by Moav (1966a,b,c, 1973) and Moav and Hill (1966). Moav and Moav (1966) also developed a profit equation for a broiler enterprise.

Step 3. Choose Breeding System and Breeds

The choice of breeding system (purebreeding or crossbreeding with specified structure) will influence the performance characteristics of the production units and the costs of producing the production animals through the expansion system of step 8. Thus, the comprehensive objective of step 2 (form B) is preferred to guide these decisions. The breeds or strains and their arrangement also need to be specified. The actual performance characteristics of production animals are determined by breeds or strains chosen for positions in the specified breeding system. Thus, the choices often can be made from the simplified objective of step 2 (form A). Either approach to decisions should find the best utilization of the alternative breeds or strains to optimize the efficiency of the production system(s).

The major alternative systems include the following: (1) purebreeding system with an established breed or strain, (2) purebreeding system with a new synthesized population, (3) rotational crossbreeding with a specified number of breeds or strains, (4) rotational crossbreeding system to produce the parent females to be terminally mated to sires of a different breed or strain (or cross), and (5) a specific terminal cross involving two or more breeds or strains. Until 40 years ago, the predominant breeding procedure for all classes of livestock was purebreeding. Since then, however, the trend has been toward systematic production systems involving crossbreeding, starting first with poultry. These changes have been prompted by recognizing heterosis or hybrid vigor for many relevant traits, especially for reproduction. Crossbreeding to exploit heterosis has been investigated widely and used in most species except dairy cattle. The earlier schemes of this list are simpler to implement, but the later ones permit greater exploitation of heterosis, average or specific, among the breeds or strains.

Breeds or strains available usually vary considerably in their characteristics: some excel in female reproductive characteristics whereas others excel in production characteristics. The use of specific crosses (alternatives 4 or 5) allows the systems designer to emphasize female reproduction in decisions concerning the parentage of dams and the growth, production, or male reproduction characteristics in decisions about the ancestry of sires. Choice of the breeding system, therefore, may involve compromises between the potential from specific crosses for heterosis, specific combining ability, and complementarity and the ease of implementation of a simpler system such as purebreeding. The difficulty of implementing crossbreeding systems (as reflected in costs of parent stock) is considerably less if the class of livestock has a relatively high reproductive rate, thus allowing more complex crosses with a low industry-wide proportion of lower performance purebred animals.

In evaluating the total system of breeding, expansion, and production, the efficiency of production by the byproduct animals should be considered. The performance of extra animals produced along with the breeding stock, but of the undesired sex, may limit the efficiency of the total system. Specific conclusions for this step should be made from experimental data that evaluates the efficiencies of different crosses in the total system. Information from several experiments may need to be combined.

If a particular crossbreeding system and a set of breeds or strains can be selected in this step, later steps will be simpler and more specific. If the performance of alternative systems does not differ enough for clear-cut decisions, some of the decisions in this step can be deferred until step 9 (comparison), in which assessment can include the effects of steps 5, 6, 7, and 8 to accomplish improvement from selection for each specific purebreeding or crossbreeding system.

Further review of the implications of crossbreeding systems as well as procedures for evaluating alternative crossbreeding systems can be found in articles by Dickerson (1969, 1973), Cartwright and Fitzhugh (1974), Fitzhugh et al. (1975), Notter et al. (1979), and Congdon and Goodwill (1980).

Step 4. Estimate Selection Parameters and Economic Weights

Develop estimates necessary to evaluate the potential of alternative schemes (steps 5 to 7) by literature search or direct evaluation. These schemes should improve the production units described in step 2 (form A) by modifying through selection the genetic characteristics of breeds or strains involved. Other forms of genetic manipulation, such as introducing exotic genes through backcross techniques or through genetic engineering, also might be evaluated. The selection parameters usually include phenotypic and additive genetic variances and covariances among the relevant characteristics specified in step 2 (form A) plus any additional traits of an individual or its near relatives to be used as indicator traits in selection criteria to be developed in step 6. When a crossbreeding scheme is chosen in step 3, the expected change in efficiency of performance of crossbreds by selection among their purebred ancestors should be described by the parameters.

Estimates necessary to predict response to selection ideally should come from experiments with the particular breeds (and perhaps the actual herds or flocks) used in the breeding system and should involve all the pertinent traits. When estimates from different populations are similar, valid estimates may be used from the research literature.

The requirements of steps 5 (evaluation) and 6 (criteria) must be anticipated to assemble the appropriate estimates. A considerable number of estimates of phenotypic standard deviations, heritabilities, genetic, and phenotypic correlations among traits can be found in the literature. These estimates are necessary to predict the response to selection for these traits or combinations of these traits within purebred populations. If the decisions in step 3 lead to a crossbreeding system, the relevant selection response pertains to improvements in the efficiency of production by crossbred animals or production units. The correlations between purebred performance appropriate for selection criteria (step 6) and crossbred performance involved in desired selection response (step 2) have not been evaluated adequately for most classes of livestock. In addition, there is a deficiency of estimates of parameters involving feed consumption, feed conversion, or the component traits of reproductive efficiency.

Kinney (1969) summarized the parameter estimates for poultry populations, and Wolde Hawariet et al. (1977) similarly reviewed estimates for beef cattle. Gaunt (1973), White (1974), and Blake and McDaniel (1978) reviewed the estimates for dairy cattle. The estimates for simultaneous selection for both dairy and beef performance have been reviewed by Miller et al. (1981).

The needed economic weights are the numerical values of the coefficients in the linear or quadratic equation that quantify the simplified objective of step 2 (form A). These numerical values needed to complete the step 2 (form A) objective depend upon the mean performance of the chosen breed or cross determined in step 3 (breeding systems). Hazel (1943) defined the relative economic weight for each trait as the amount by which profit may be expected to increase for each unit of improvement in that trait. Harris (1970) made this definition more mathematical as the partial derivative of the aggregate genotype (step 2, form A, simplified objective) with respect to each trait evaluated at the point of the mean genotypic values. Both these definitions are consistent with the operational procedure suggested in step 2, form A if the μ values in the weights are taken to be the means for the specific traits of the production units (possibly crossbred) specified in step 3. We find it appropriate at this point, therefore, to combine the formulation of step 2, form A, with the means for step 3 to yield the economic weights needed for steps 5 through 7, but especially step 6 (criteria).

Step 5. Design Animal Evaluation System

Subject to constraints of reproduction and longevity, an evaluation system should be designed to measure and record relevant characteristics at appropriate times to include in the selection criteria in step 6. This testing system involves specifying the life cycle of test animals (along with the life cycle of their near relatives such as sibs or progeny) with measurements to be taken before possible multiple points of selection and breeding. Life cycles are not necessarily the same for individuals of different sexes, and they must be arranged so that appropriate numbers of each sex are available for mating at the appropriate time. When step 3 leads to a crossbreeding system, the various breeds and strains in the optimum cross may require different testing, selecting, and mating systems (steps 5, 6, and 7), especially the sire breeds in contrast to the dam breeds.

The specification of life cycles for an evaluation system should include the following:

1. Ages (and weights, or both, or other details) at which measurements are taken.
2. Traits (direct or indicator, or both) measured and recorded at each specified age.
3. Appropriate ages (or other points) in life cycle where selection **might** be made. (There might be only one point, but there often should be multiple points to

allow for potential advantages of multistage selection.)

4. How long, or until what later selection (or culling) point, selected animals are to be used in a breeding flock or herd to reproduce the strain or breed.
5. Environments or other special characteristics that might be imposed, such as sib or progeny testing following disease exposure.

Characteristics of importance will fit into five general categories.

1. Characters such as birth weight, weaning weight, or postweaning growth rate are easily measured on each individual with little cost.
2. Some characters, such as age at puberty and individual feed efficiencies, are easily measured but require additional labor or special facilities.
3. Other characters can be measured only if the animal reproduces, for example, fertility, fecundity, birth weight, and maternal characters.
4. Additional characters such as carcass characters or merit of sires for maternal performance, cannot be measured on potential breeding animals and must be observed on relatives.
5. Characters that cannot be measured until after an animal has completed its reproductive life, e.g., longevity, lifetime measures of fertility, and offspring weight-production characters. Characteristics in this last category can be evaluated only through information from ancestors or indicator traits.

If breeding population size remains constant over generations, the proportion selected (which must be decided in step 7) is determined by the average number of offspring of the same sex produced by the selected animals. For selection to be intense, animals should be chosen early in life so they have a long reproductive life after selection. Early selection considerably limits the potential for evaluating and selecting for long-term reproductive characteristics. Thus, possible decision making in step 7 needs to be allowed for in this step.

Different types of alternative evaluation schemes may be considered. For example, alternatives might differ by the presence or absence of progeny tests and by whether progeny tests are purebred, crossbred to a tester, or reciprocally crossbred. Thus, more than one type of scheme or system may have to be considered with steps 6, 7, and 8 developed separately for each, and the decision among these alternatives deferred until step 9 (comparison). Often, the life cycle of test animals will be similar to the life cycle of the production animals as described in step 1 (production system). The test animals, however, may have altered life cycles so as to facilitate measurement of relevant characteristics. For example, the normal age of mating for reproduction may be delayed if mating would interfere with the measurement of such germane characteristics as growth rate to a marketing age later than the age normal for mating. Departures from normal production and management life cycles, however, may allow genotype-environment interactions that might reduce the effectiveness of selection.

Multistage selection should be considered when there are many traits measurable at different stages in the life cycle. Multistage selection will allow more effective use of the evaluation resources since only animals with adequate performance for a trait expressed early in life, such as growth rate, need be evaluated for traits expressed later, such as reproduction. We suggest, therefore, specifying possible multiple selection points.

Data from the production system might be useful to the testing system. For example, some or all production animals could provide progeny test information on their parents such as for dairy sire evaluation. Deciding to use such information depends on the nature of the genetic connection (intervening generations) between the testing system and the production system. This relationship will have to be specified in step 8 (expansion). The relative merits of progeny testing versus direct observations are described by Dickerson and Hazel (1944).

Ideally, information should be available through either direct measurement or measurement on near relatives concerning all the characteristics relevant to form A of step 2 for each animal that is a candidate for selection. Some difficult or expensive-to-measure traits, such as feed consumption, might be excluded, but only if adequate prediction of that trait is possible from other traits measured. Since the set of observable characteristics may not be the same for the two sexes, and since the relative importance of the component traits may differ, depending upon how the breed or strain is used in a cross, different testing schemes may be needed for each sex of each breed. The life cycles must be arranged, however, to have appropriate numbers of each sex available for mating at the appropriate time for reproducing the herd or flock (step 7) and to have appropriate numbers of animals available at appropriate times for the expansion scheme to be developed in step 8 (expansion). Some anticipation of step 8 will allow for reproduction contributing to the expansion scheme in addition to reproducing the next generation of animals to be candidates for selection.

Step 6. Develop Selection Criteria

Each selection criterion should be developed as an appropriately weighted mathematical function of the relevant direct and indicator traits of individuals and near relatives. Only observations made before that selection point in the cycle can be used. An optimum selection index should be used in preference to simpler criteria. The decision among the selection criteria possible at a specific point in the life cycle should maximize selection response in the simplified objective of step 2 (form A), using economic weights from step 4 (estimate). This decision is more complex than is often realized. It should result from the prediction of selection response in both efficiency of lifetime parental reproduction and efficiency of production in (crossbred?) progeny when the selection is made on the basis of production traits expressed early in life in purebred populations. In step 6 (criteria), a selection criterion should be developed for each selection point in step 5 (evaluation), for each sex and, possibly, for each breed or strain.

This step is closely allied to the previous step and will often be developed simultaneously. The number of different selection criteria depends on the stages of selection specified in step 5 (evaluation) and the sexes and breeds for which there are differing selection life cycles. Short-cut procedures may be considered until better estimates are available if available estimates of the necessary parameters are not adequate. For multistage selection, the optimum index at each point utilizes all available information even if some information was used in previous selections (Cochran 1951).

An essential part of the selection criterion would be adjustment factors, such as those for age-of-dam effects, to correct for identified extraneous environmental variation to make the selection criteria more accurate. Henderson (1973) has presented best linear unbiased prediction (BLUP) as a procedure for simultaneously predicting breeding values and adjusting for fixed effects. The use of BLUP genetic evaluations in conjunction with quadratic bioeconomic objectives (Wilton et al., 1968) seems most appropriate. The most pertinent basis for deciding among selection criteria is to choose the one that will maximize selection response at that specific point. This basis requires maximizing either the predicted one-generation selection response for the simplified breeding objective (step 2, form A) for a specific intensity of selection or, equivalently, maximizing the correlation between the selection criteria (for purebred candidates for selection) and the additive genetic value for that objective (may be for crossbred performance). James (1978) developed the theory for developing indexes to improve simultaneously both current and future generation gains.

At each selection point, the choice should result in the cirterion that will give the greatest response towards the objective. The decisions are highly dependent, therefore, upon the reliability of the predicted response. This reliability, in turn, is dependent upon the accuracy of the parameter estimates and their specificity for the breed or strain being selected. The lifetime aspects, crossbred aspects, and efficiency aspects of a complex bioeconomic objective have been frequently neglected in developing parameter estimates. Decisions in steps 7 (mating) and 8 (expansion) are also affected by these complications, so the inadequacy of parameter estimates will lead to difficulties and limitations in developing adequate selection proportions and multiplication schemes.

Many research workers have developed selection criteria for numerous definitions of objectives in various species. Among them are Soller et al. (1966), who considered simultaneous selection for growth rate and milk production in dairy cattle, and Cartwright (1970), who considered appropriate selection criteria for beef cattle. These two studies go further in applying a systems perspective to developing economic weights for index construction than most uncited references on this topic.

Step 7. Design Matings for Selected Animals

Include in this portion of the design the proportions to be selected at each selection point for the life cycle of each sex of each breed or strain, keeping in mind that an adequate number of selected males and females should be available for mating at the specified breeding seasons for reproducing. Designing the mating system includes deciding among inbreeding, assortative mating, or random-mating strategies. Inherent in these decisions are the specification of the mating ratio of females to males and the number of breeding seasons to be used for selected individuals. Where variation is possible, the length of the breeding season (for example, number of weekly hatches in poultry) should be specified. Decisions on the design of the mating system should maximize the overall genetic response in the simplified objective from step 2 (form A). The primary goal of designing breeding population sizes should be to maintain a population large enough to sustain sufficient genetic variability for long-term response to selection. Adequate population size is also necessary for stable responses and for supporting the expansion system specified in step 8 (expansion).

Many of the principles of this step are contained in the work of Dickerson and Hazel (1944), and these have been added to by Robertson (1957), Smith (1959, 1960, 1969, 1981), and James (1972).

In this step, the breeder needs to decide how to reproduce from the selected males and females for producing a next generation of test animals. Step 5 (evaluation) should have been developed so that males and females are available for mating (step 7) at an appropriate time shortly after final selection. In this step, the breeder should decide on the appropriate numbers of selected males and females.

These decisions affect the intensity of selection that, together with the accuracy of selection (the correlation between selection criterion and selection objective) and the generation interval, decide the rate of change achieved from the additive genetic variability present within the breed or strain. The accuracies were determined, and hopefully maximized, by the selection criteria decisions in step 6. The generation intervals were largely determined by the life cycle specifications for an animal evaluation system in step 5. How many breeding seasons to utilize the selected animals is to be decided in this step, which also influences generation interval. Timely reproduction after selection helps to keep the generation interval short to increase the rate of genetic improvement over time. Length of reproduction in terms of the number of breeding seasons the selected animals are utilized, however, greatly controls the proportions that can be selected. In addition, the length of reproduction determines the number of sib relatives that can influence the accuracy of selection. Thus, the decisions should lead to selection proportions that maximize the overall rate of genetic response from selection at all stages in the life cycle. This overall rate of genetic response is reflected in the following formula:

$$\frac{\Sigma\Delta \mathbf{G}_m \mathbf{p}_m + \Sigma\Delta \mathbf{G}_f \mathbf{p}_f}{\Sigma\ \mathbf{t}_m \mathbf{p}_m + \Sigma\ \mathbf{t}_f \mathbf{p}_f} \qquad (3)$$

where

ΔG_m represents the expected genetic change in males for the objective for a specific breeding season (combined effect of prior stages of selection),

ΔG_f represents a similar value for females,

p_m represents the proportion of a male's offspring that are produced in each breeding season he is utilized,

p_f is similar for females,

Σ represents the summation of these products over breeding seasons,

t_m is the age of parent males for a specific breeding season,

t_f is a similar value for females.

In the simplest form,

$$\Delta G = i \, \rho_{GI} \sigma_G$$

where

i is the selection differential expressed in standard deviation units (reflecting the intensity of selection) and will be greater for smaller selection proportions.

ρ_{GI} is the coefficient of correlation between the selection criterion (I) and the additive genetic value for the bioeconomic objective (G) (this reflects the accuracy of the selection criterion),

σ_G is the standard deviation of the additive genetic values for the combined traits in the bioeconomic objective (this reflects the genetic variability available for selection).

The choices to be made in this step lead to specification of the **i**, p_m, p_f, and ranges for the Σ in these formulas. The formula for ΔG is strictly true when the criteria and the objective are linear or quadratic functions of normally distributed component traits and the selection is single stage. The principles expressed are still relevant, however, when more complex selection criteria are involved. A more complex formula is necessary to describe progress for multistage selection.

Step 7 (mating), along with steps 6 (criteria) and 8 (expansion) should be repeated for each alternative type of testing scheme specified in step 5 (evaluation) and may be repeated for each breed or strain specified in step 3 (crossbreeding). At this point, one ideally should include in the plan a system for monitoring and verifying selection progress in the strains or breeds (or both) selected.

An excellent example of applying the principles of this step and step 8 (expansion) to dairy cattle is contained in the study by Skjervold (1963). Related applications to beef cattle were considered by Cartwright et al. (1975).

Step 8. Design System for Expansion

Design a system so that genetic improvements developed in the testing, selecting, and mating system can be disseminated into the production system(s) effectively and economically. Genetic improvements can be transferred and expanded concurrent with crossing of the improved strains or breeds to produce male and female parent-breeding stock or by using artificial insemination (AI) to sire production animals. The choice of transfer strategy also necessarily involves breeding population size and should be consistent with decisions made in step 7 (mating). The decision requires consideration of both the number of improved animals produced **(mass)** and the expected genetic improvement **(magnitude)** in an average production unit, that is, the simplified objective (step 2, form A). To include the costs of expansion and crossing, the comprehensive objective (step 2, form B) should be used. The benefits (= **mass** × **magnitude**) relative to costs are of primary concern. The choice should lead to maximum net benefits in the total system so there will be an adequate return on investment.

The principles involved in the decisions for this step are clearly stated by Bichard (1971). For most classes of livestock, effective selection for genetic improvement occurs in only a small fraction of the herds or flocks with production occurring in a larger fraction of the total industry. An intervening segment of the industry is necessary, therefore, to disseminate the genetic improvements being made in the leading selection herds or flocks to a large number of production herds or flocks. This expansion is done most systematically in the poultry industries where grandparent flocks produced from the selection flocks are maintained to produce the parent-breeding stock, which in turn produces the commercial broilers or egg-laying stocks. These grandparent flocks are expanding the **mass** output of improved stocks from the selection program to provide adequate numbers of parent stock for the poultry industries. This expansion phase is done in conjunction with the initial crossing when the final production animals are three- or four-way crossbred individuals. This increase of **mass** is accomplished by a one-generation delay in the **magnitude** of genetic improvement reaching the production phase. The large potential for expansion can exceed the loss in economy from the delay considerably.

The expansion or multiplication phase for the larger meat production animals has not been as distinctive, but its role is partially served by those breeders (possibly not practicing an intensive selection program) who purchase their breeding stock from the more effective breeders and largely derive their income from sale of progeny as breeding stock to commercial producers. In the larger meat animals, the breeding stock involved in the transfer from the superior breeders to the multiplier breeders and from

multipliers to the producers is usually only male breeding stock (or AI semen) with female replacements raised within each herd or flock and retained for further breeding. With only the male sex involved in the expansion, the increase of **mass** of improved animals will be partially offest by a halving of the **magnitude** of genetic improvement, but the potential increase in mass can lead to an increase in **mass × magnitude.** Superior breeding programs based upon decisions made in steps 5, 6, and 7 will affect the industry only through an effective system for conveying these genetic improvements to influence the production segment of the industry. There is considerable opportunity for improvement of this aspect in most of the animal industries.

The expansion possible with AI has been a prime basis for improved procedures of genetic selection in the dairy cattle industry. This technique for enhancing reproduction ability has its impact on dairy breeding in (1) greater accuracy of evaluation for steps 5 and 6 by facilitating sire evaluation by multiherd progeny tests, (2) greater intensity of selection among progeny tested sires possible in step 7, (3) and an enhanced expansion system for disseminating the genetic improvements in a single generation to improve the production efficiency of dairy animals. Future advances in reproductive capabilities have the potential for similar influences upon the other animal industries. For example, embryo transfer or cloning could be utilized similarly if further developments can reduce the costs of these techniques to an economic level similar to the costs of AI.

Thus, an organized system of expansion appears mandatory for the practical impact of genetic selection and breeding. Much effort is required in designing multiplication systems that will be efficient. With a segmented industry, a financial feedback from the production system should reimburse the breeding system for its expenses and for its improvement contributions to the production system. In industries with many participants, this financial feedback is the necessary basis to motivate the elite breeders leading the genetic manipulations of the total system. Of course, the **mass** produced by the multiplication system must have a reasonable expectation of use or sales.

At this point, the breeder should consider again the associated production systems of step 1 (production systems) that were judged to be secondary in step 2 (form A or B) when a singular major or average production system was chosen as the target in defining the objective for the breeding program. The breeder should decide whether those production systems that departed in some details of scheduling, climate, marketing, and so forth, can receive an adequate benefit from correlated responses to selection. The correlated responses pertinent to secondary production systems are likely to be less than those for the primary system because of genotype-environment interactions. When the expected correlated responses are inadequate, other breeding systems should be developed to support these alternative production systems. Separate breeding systems for separate production systems within the same industry may not be cost-effective because of the smaller market to be influenced by each breeding system. The concern should be whether some minor production systems are financially large enough to support secondary breeding systems or whether the minor systems should be content with the genetic improvement resulting from correlated responses from a primary breeding system targeted towards a larger production system.

Step 9. Compare Alternative Combined Programs

This final step completes the comprehensive decisions in designing the breeding program. If information or formulations were not complete enough in earlier steps to allow clear-cut decisions, the planner should return to these earlier steps and develop them more fully before proceeding with step 9.

Sometimes the final decision concerning the breeding system and breeds should be deferred from step 3 until this step. In this way, the final decision can be made not only on the merits of the breeding system as a specific part of a total production system but also on how that purebreeding or crossbreeding system interacts with steps 5 to 8, allowing for improvements of the production system through selection. The designer also may have deferred decisions among some testing schemes in step 5 to be evaluated further after the contributing choices were made for each in steps 6 to 8. In fact, the step 5 decisions will be subjective rather than objective until steps 6 to 8 have been optimized.

The potential branching to alternative choices in earlier numbered steps is represented in figure 2, where arrows indicate the flow of thought processes for designing the breeding program. At this final step, the branches converge to represent the comprehensive comparisons and final choices that will be made among the combined programs. Some choices will have been made in the intermediate steps concerning optimum schemes for each branch in figure 2. For example, the optimum selection criteria should be developed in step 6 for each animal evaluation system of step 5. Similarly, the optimum selection proportions at each stage of the evaluation system probably will be decided as a part of step 7 (mating). The more comprehensive decisions between alternative schemes may have been deferred to step 9 for many of the steps, but we find that most of the deferred alternatives will be for steps 3 (breeding system) and 5 (evaluation).

The relative cost of alternative breeding programs can become a part of this comprehensive evaluation, whereas such costs may have been neglected in the decisions made for a specific step using the simplified selection objective of step 2 (form A). The decisions in step 9 should be based on relative benefits and costs. These benefits should reflect the **mass × magnitude** of the genetic improvement of overall production efficiency and the costs include the combined functions of selecting, expanding, crossing, producing, and processing as described in step 2 (form B). Many practicing animal breeders will require

the help of technically trained animal breeders. These trained breeders will need computer calculations based on methods of systems analysis coupled with quantitative genetic and animal-breeding theory.

Many of the references mentioned are also relevant to this step. In addition, the designer of breeding programs should consider the work on group breeding schemes in New Zealand and Australia described by Jackson and Turner (1972), Rae (1974), and Jones and Napier (1980). Two other noteworthy papers applicable to several of the described steps are by Cartwright (1974) and Long et al. (1975).

Sequential Aspects and Iteration

The rationale behind the recommended sequence of these nine steps involves the later-numbered steps that require information from some earlier step(s) or that depend on decisions made in earlier steps. As stated earlier, sufficient anticipation of the later steps is necessary to develop properly the information necessary for these steps. In addition, the decisions in the earlier steps should be made in a broad context so that the decisions in the later steps are not restricted. Sometimes compromises may be necessary between steps 7 (mating) and 8 (expansion). Except for these compromises and some arbitrariness in the order of steps 6 (criteria) and 7 (mating), the sequence chosen resulted from a natural flow of information and decisions through the first eight steps with a ninth comprehensive decision making step.

At the beginning of step 9, we suggested that the decision maker might return to earlier steps and develop them adequately before completing this step. Each step, however, does not need to be completed before initiating work and thought processes on a later step. The natural sequence really only requires that an earlier step be completed before a later step can be completed. Even though the sequence is natural, the person or group making the decisions probably will prefer to work through the first eight steps in an iterative manner with several repeated passes. The iterative approach will facilitate the fitting together of the various steps (fig. 2).

Systems Analysis

Systems analysis recently has received considerable attention as an appropriate tool for comparing many types of agricultural systems. General reviews of these approaches are included in von Bertalanffy (1951), Dent and Anderson (1971), Jones (1973), Spedding (1975), Roundtree (1977), and Dent and Blackie (1979) with tools specifically pertinent to animal breeding reviewed by Brascamp (1978).

We have used this nine-step approach as a guide for developing a computer model of breeding systems designed to analyze systematically the many alternative breeding plans for broiler chickens. We hope to follow this publication with others that deal with more specific breeding problems encountered in each of the recommended steps for the major classes of livestock. Computer

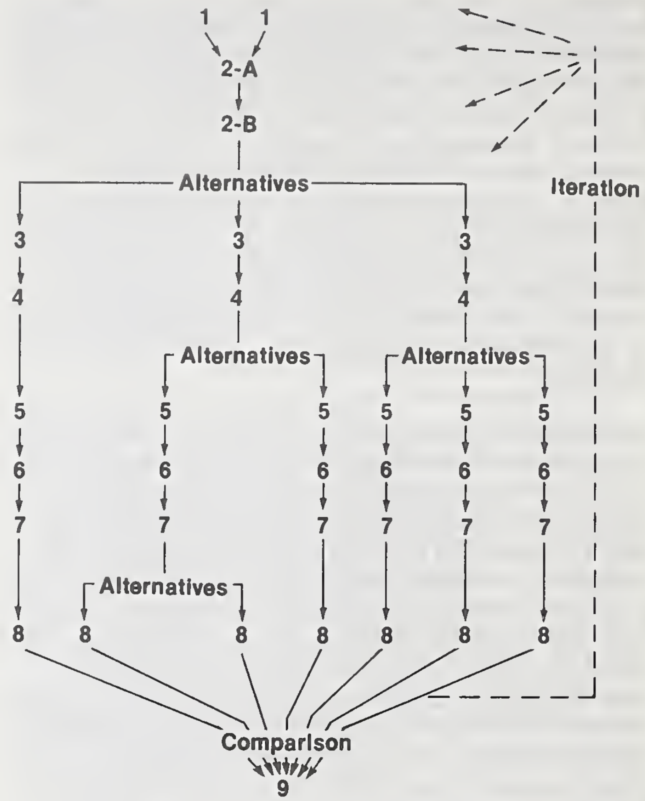

Figure 2.—The flow (solid arrows) of decision making through the steps with branching for alternatives to be resolved in comparisons of step 9 and with iteration (dashed arrow) back to earlier steps to modify the development.

models in conjunction with this systematic approach are intended as a basis for fully integrating relevant research and knowledge into meaningful procedures. In this way, systems analysis can be used to unify the existing concepts and theories of breeding and genetics and the practices of animal production to form more rational and effective animal-breeding programs.

The computer model for broilers was developed by a series of iterations of the first eight steps, followed by a comprehensive computerized step 9 to compare the many alternative combined programs. The series of iterations comprised (1) conceptualizing the necessary details of each step, (2) reviewing the scientific literature to find relevant theory and methodology, (3) extending theory and methodology as needed for completing the modeling, (4) developing appropriate algebraic representations, (5) programing the appropriate computer simulation procedures, and (6) executing the computer program to make the numerical comparisons of the alternative schemes judged to be potentially valuable. The results of these activities will be reported in other publications.

Computer modeling allows the use of more complex calculations towards a more complete system objective (step 2, form B) for the more comprehensive decision making proposed for step 9.

Future Modifications

Even a well-designed animal-breeding program is unlikely to remain static for long. Numerous potentially changeable influences impact upon a breeding program. They include changes in the economic and marketing situation, changes in the availability of outside germplasm, changes in the methods and procedures of evaluation developed in ongoing research, and changes in reproduction technology. In general, future changes will require additional iterations through the stepwise procedure, leading to modifications in the design of the breeding program.

A small change in economic situations in the marketplace or in the cost of feed or other inputs into the production system may be met by simply redoing steps 4 (parameters and economic weights) and 6 (criteria). A large change in the economic situation of the industry may require a return to step 2 (objective) to refine the objectives followed by reevaluating and recalculating the details of all the remaining steps. It also may lead to large enough changes in management and other aspects of the production systems so that all steps, beginning with 2 (production system), will need to be redone. The availability of new germplasm would lead to a return to step 3 (breeding system) to reevaluate the alternative breeding systems and possible changes in the breed composition. This new germplasm might also require new estimates of parameters of selection in step 4 (estimation) relevant to the new breeds, and this, in turn, would lead to reevaluation of all the later steps.

As research leads to new parameter estimates, an additional iteration back to modify steps 4 (estimation) and 6 (criteria) would be in order. When research brings about a suggested change in the method of evaluation, such as identifying new indicator traits, an iterative return to steps 5 (evaluation) and 6 (criteria) to redesign the animal-evaluation system and to develop new selection criteria would be required.

Changes in reproduction technology (such as of embryo transfer) could have several effects on the system. They might allow a different system of expansion in step 8, greater intensities of selection in step 7, or more accurate progeny tests in steps 5 (evaluation) and 6 (criteria). The changes may even lead to different breeding systems in step 3 since increased reproduction could facilitate more complex breeding systems. New reproductive technologies should be evaluated on calculations indicating the impact of the technique upon the total system with emphasis on cost effectiveness.

Segmentation of the Industry

Up to now, our discussion has been written as if one person or group was making the decisions through all nine steps. The coordination necessary for efficient and balanced decision making would be more likely with a single decision maker. This unity of decision making, however, has been achieved only in some highly integrated broiler chicken operations where the same corporation is involved in all aspects and functions of the system from selection through processing. This high degree of integration has not been achieved in most other classes of livestock and objectives. Many people or organizations are involved and make decisions in each of the six functions shown in figure 1. Each participant will represent different resources and serve various roles (primary breeder, multiplier breeder, or commercial producer), and will likely arrive at different conclusions for many of the steps. Directing different production systems towards different resources may require or allow different crossbreeding systems or breeds to be used. Choices may even be made to allow one breed to have different roles in different production systems. The nature of the evaluation system and, thus, the selection criteria may change, depending upon the resources of a specific breeder. With such varied and often contradictory conclusions, developing a systematic, integrated design has been difficult.

A variety of approaches have characterized the large animal industries in the past and, in many cases, have made the impact of animal-breeding programs on commercial production quite small in comparison with the potential. Some differences may be justified if based upon different relevant facts about the resources and roles. The animal-breeding industries also have been hampered by many subjective opinions about the details of breeding systems, the nature of desired changes in characteristics of breeds, and how to conduct selection programs. The greatest hindrance to many breeding programs has been the lack of an accurate definition of the objective of the overall breeding program.

If animal-breeding programs are ever to be fully effective, the limitations from this segmentation must be overcome. Segmentation has been overcome in some countries by centralized control of breeding operations—an approach that is totally unacceptable in other countries. In some classes of livestock, vertical integration has brought about centralized control. The alternative to centralized control comes through the cooperation and coordination of many smaller breeders and producers. Breed associations and other industry organizations, therefore, might serve as the forum for such communication and coordination. The suggested degree of coordination and cooperation may seem difficult, but sufficient agreement by a large segment of a specific industry could allow concerted action if the rewards are adequate for all participants. Improving the efficiency of animal production would benefit not only the developers of that improvement but also all other segments of the industry, including the consumers of animal products.

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